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# Carbon and nutrient dynamics in decomposing pine needle litter in relation to fungal and faunal abundances

**Motohiro Hasegawa and Hiroshi Takeda**

Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Kyoto 606, Japan

**Summary.** Decomposition processes of pine needle litter were studied in a pine forest with a moder humus form using the litter bag method and were followed in terms of carbon and nutrient dynamics (N, P, K, Mg, Ca) and fungal and soil animal population dynamics over a four year period. Decomposition rates of pine needles decreased with the field exposed time and were significantly higher in the first year ($k = 0.467$) than in the rest of the experimental period. Changes in carbon and calcium mass were similar to those in needle weight loss, while the changes in nitrogen and phosphorus mass showed three phases; (1) leaching loss (0 – 3 months), (2) initial net immobilization (3 – 9 months) and (3) the steady-state phase (12 – 48 month). Potassium and magnesium mass rapidly decreased through leaching. Fungal colonization was characterized by three stages; stage 1: growth (3 to 9 months), stage 2: steady-state (12 to 18 months), and stage 3: collapse (21 to 48 months). During stages 1 to 2, fungal growth contributed to the immobilization of nitrogen and phosphorus in the needle litter. The litter bag fauna was dominated by Cryptostigmata (33.7% of total population), and Collembola (31.6%). Total soil arthropod densities increased with the decomposition process of needle litter and the densities of total soil arthropods and Cryptostigmata were significantly correlated with C/N and C/P ratios during decomposition. The soil microarthropods contributed to the immobilization process of nitrogen and phosphorus through their grazing activities in the early decomposition phase (0 – 18 months) and the recycling of faeces and decomposition products in the late decomposition phase (21 – 48 months).

**Key words:** Decomposition, carbon and nutrient dynamics, fungal abundance, soil arthropods, Cryptostigmata, Collembola

## Introduction

The successional changes of soil organisms have been demonstrated during the decomposition process of various litters using litter bag methods (e.g. Anderson 1975; Berg & Söderström 1979). The roles of soil organisms on carbon and nutrient dynamics may be changed during decomposition processes in soils (Hasegawa & Takeda 1995). Among nutrients, nitrogen dynamics of decomposing litter showed leaching, immobilization, and mobilization phases (Berg & Staaf 1981; Takeda 1995) and have been related to the activities of microbial populations (Berg & Söderström 1979). The functional roles of micro-arthropods are indirect on decomposition processes and have been mainly attributed to their grazing effects on the microbial populations in the immobilization phase (Petersen & Luxton 1982).

Soil microarthropods are abundant animal groups in the mor or moder humus forms and consist of various animal groups, including Cryptostigmata (Wallwork 1967; Luxton 1972;

Siepel & Maaskamp 1994) and Collembola (Hågvar & Kjøndal 1981, Takeda & Ichimura 1983; Faber 1991). The roles of these arthropods on the decomposition of litter may be changed during the decomposition phases of litter. Collembola and Cryptostigmata contribute to the immobilization by their grazing in the early decomposition phase and the mobilization of nutrients in the late decomposition phase in the moder humus form (Hasegawa & Takeda 1995; Takeda 1995). But there have been few studies on the roles of soil animals in the late decomposition phase.

Most decomposition studies have followed changes in soil faunal and microbial abundances in relation to nutrient and carbon dynamics over only one or two years period, so long-term research is required to reveal the complete decomposition processes of leaf litter, especially in mor and moder humus forms where decomposition may be a slow process (Staaf and Berg 1982; Edmonds 1984; Takeda 1988, 1995). Further long term joint studies between litter, micro-flora and micro-fauna are needed to understand the roles of soil animals in decomposition processes.

The objectives of the present study were to show the pattern of pine needle decomposition in terms of nutrient dynamics (C, N, P, K, Mg, Ca) and fungal and soil animal population dynamics over a four year period in a coniferous forest soil with a moder humus form, and to assess the role of soil fungi and arthropods in the decomposition phases of *Pinus densiflora* needle litter.

## Materials and Methods

### *Study area*

The study was carried out in a natural forest of Japanese red pine (*Pinus densiflora* Sieb. et Zucc) mixed with *Chamaecyparis obtusa* Endle at Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of Kyoto city (35.04′ N and 135.43′ E). Details of the study area have been reported in Takeda (1976, 1978). A study plot of 10 m × 10 m in area was laid out in the pine forest. Meteorological records were obtained from the Station. Mean annual precipitation and evaporation were 1,678 mm and 985 mm respectively. The surface litter layer often dries out in May and mid summer. The soil humus form in this study area is a moder with a poorly developed mineral soil horizon (A) which is about 1 cm in thickness. The $A_0$ layer consists of L, F and H layers, ranging from 2 to 5 cm in thickness. The transition between the H and A layers is indistinct, but the boundary between the A and B layers is very sharp. The $A_0$ layer is the main habitat for the soil microarthropods in this study area (Takeda 1976).

### *Litter bag methods*

Decomposition processes of pine needle litter were studied by a litter bag method (Crossley & Hoglund 1962). Newly fallen needles of *Pinus densiflora* trees were collected from the forest floor in December 1989. Litter bags (Each 10 cm × 10 cm in area with a mesh size of 3 mm) were used for the decomposition study. Three grams of air-dried pine needles were placed in each litter bag. This litter mass approximated the litter falls in this study area (Takeda 1988). Samples of initial and decomposing needles were dried at 80 °C to a constant weight.

The litter bags were set out in a 10 m × 10 m study plot divided into 10 suplots each 2 m × 5 m in area. A 1 m × 1 m area was laid out in each subplot to contain 20 litter bags. Litter bags were placed on February 29, 1990. After the removal of newly fallen litter, the litter bags were fastened to the forest floor by metal pins to prevent movement and to ensure a good contact between the litter bags and the organic layers.

Litter bags were collected every 3 months from May 1990 to February 1992 and were collected in February 1993 and 1994. On each sampling occasion from May 1990 to February 1992, 20 litter bags were collected from the study plot (i.e. 2 litter bags were collected from each sub-plot), returned to the laboratory, and used for the study of soil animal populations, fungal colonization, and chemical analysis of litter. On the sampling occasion in February 1993 and 1994, 10 litter bags were collected.

*Chemical analysis of needle litter*

After the extraction of soil animals, samples of litter were used for chemical analysis. Samples of initial and decomposing needles were dried at 80 °C to a constant weight and ground in a laboratory mill to pass a 0.5 mm screen. Total nitrogen and carbon of pine needles were measured by automatic gas chromatography (C−N corder, Yanagimoto Co., Japan). After an acid wet oxidation in $HNO_3 + HCLO_4$ the following analyses were performed; vanad-yellow method for P, flame photometry for K, atomic absorption for Ca and Mg.
The decomposition rate of needle litter was estimated using the exponential decay model of Olson (1963); $DM/DM_0 = \exp(-kt)$ where k is the decay constant, t is the year, $DM_0$ = original mass of dry matter, DM = mass of dry matter after a given period. Carbon and nutrient contents of litter after a given period of decomposition were calculated by the following formula; Remaining mass (percentage) = $C/C_0 \times DM/DM_0 \times 100$, where $C_0$ = initial concentration of nutrients (N, P, K, Mg, Ca) or carbon in litter and C = concentration of nutrients or carbon after a given period.

*Estimation of hyphal lengths*

Fungal abundances were estimated during the decomposition processes of needle litter over a 4 year period. On each sampling occasion of the first 2 years, 10 of the 20 litter bags collected were used for the estimation of fungal abundances after extraction of the soil animals. On the sampling occasion of the 3rd and 4th year, 5 of 10 litter bags were used. In this study, both the hyphal lengths of the surface and internal tissues of the pine needles were estimated in the first 2 years. Hyphal lengths of the 36 and 48 months needles were estimated without separating those of the surface and internal tissues, because the fragmentation of needle litter had advanced. The hyphal lengths of the surface of needle litter were estimated at 3 monthly intervals during the study period, whereas hyphal lengths of the internal tissues of the needle litter were estimated on four occasions, i.e., May and November in 1990 and 1991.
To estimate the hyphal lengths both on and within the needles, one gram of pine needles was boiled with distilled water for an hour. Then the surfaces of needles were rinsed by an ultrasonic washer to ensure the collection of fungi from the needle surfaces. The rinsed needles were used for the estimation of fungi colonizing them interiorly and the rinse water was used for the estimation of fungi colonizing the needle surfaces. The hyphal lengths were determined by using a modified membrane filter method (Hanssen et al. 1974). Details of the method of hyphal length estimation are shown in Hasegawa and Takeda (1995).

*Soil animal populations*

Changes in soil animal populations were studied by litter bag methods. On each sampling occasion, twenty litter bag samples were collected during the first 2 year period and were used for the estimation of soil animal populations. On the sampling occasions of the 3rd and 4th years, 10 and 8 litter bags were collected respectively. Soil animals in the litter bags were extracted by a modified Tullgren funnel at a constant temperature of 35 °C in a cabinet for 3 days. Animals were collected in 99% ethanol. Identification, counting and measurement of soil animals were carried out under a binocular microscope with a magnification of 400 X.

## Results

*Change in the litter mass and water content during decomposition*

Fig. 1 (a) shows the changes in dry weights of pine litter over a 4 year period from February 1990 to February 1994. About thirty three percent of the original mass remained at the end of the experiment. Decomposition rates of pine needles were expressed by the decomposition constant of Olson (1963) (Table 1). The decomposition rates decreased during the field exposed time and were significantly higher in the first year than in the rest

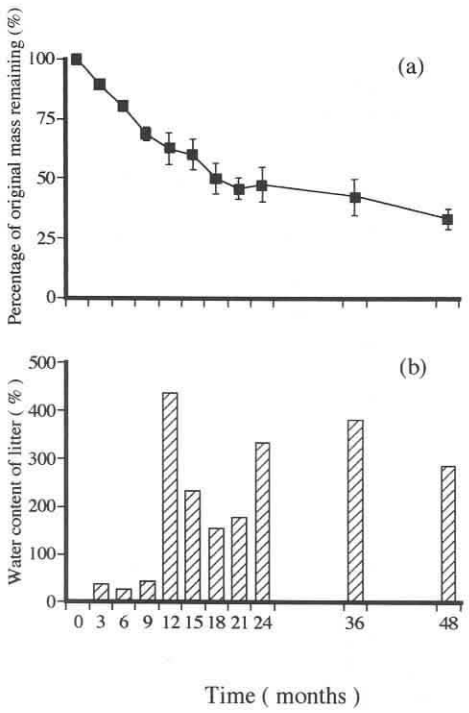


**Fig. 1.** (a) Percentage of original mass remaining of pine needles during the decomposition process. Bars indicate standard deviations. (b) Changes in water contents of litter during the study period

of the experimental period. Changes in water contents of pine litter were monitored over a 4 year period and are shown in Fig. 1 (b). In the first 9 months, water contents ranged from 50 to 60%. Water contents of needle litter increased sharply after the end of the litter fall period in the winter of 1990, then water contents of litter ranged from 150–450% through the rest of study period and were maintained by the coverage of newly fallen litter on the litter bags.

*Nutrient dynamics in needle litter*

Fig. 2 shows the changes in carbon and nutrient mass during the study period as the percentages of the initial dry mass. Changes in carbon mass were similar to those in weight loss, while the changes in mass of nitrogen and phosphorus showed three phases; (1): leaching loss in the first 3 months in both nitrogen and phosphorus, (2): initial net immobilization during 3 to 9 months in both nitrogen and phosphorus, and (3). the steady-state phase during 12–48 months, no mass change in nitrogen and gradual increase in phosphorus.

**Table 1.** Decomposition rates for *Pinus densiflora* needles over a 4 year period

| Time (treatment) | Decomposition rate (k) |
|---|---|
| 0–1 year | 0.467 |
| 0–2 year | 0.374 |
| 0–3 year | 0.288 |
| 0–4 year | 0.276 |

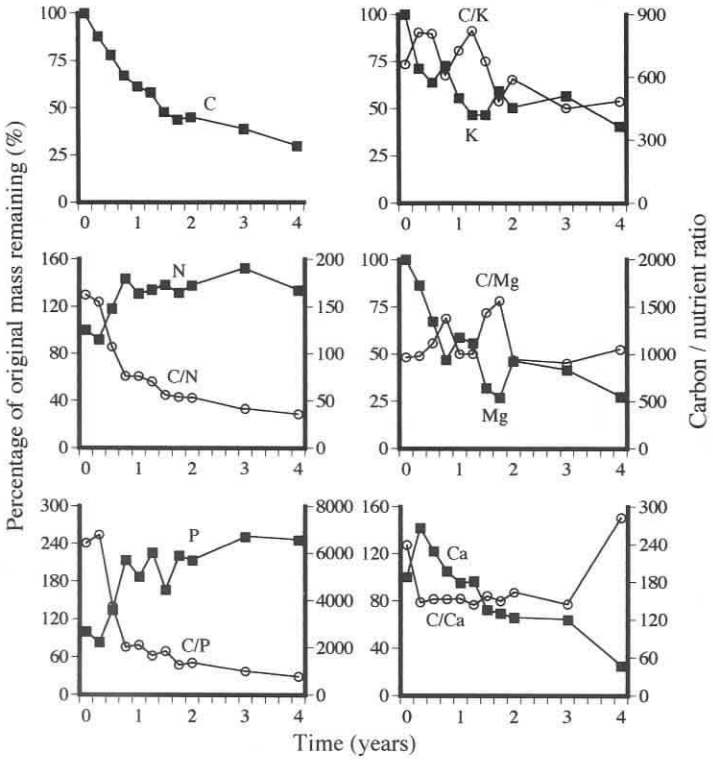


**Fig. 2.** Changes in absolute amounts of nutrients in pine needle litter during decomposition (Values are shown as the relative proportion remaining of initial amounts of each nutrients.) and carbon/nutrient ratios of needle litter during decomposition

In the first leaching phase, nitrogen and phosphorus mass decreased by about 7% and 6% of the original amounts, respectively. During the initial net immobilization phase, nitrogen and phosphorus mass increased to 145 and 200% of the original mass, respectively. Finally the nitrogen mass was in steady-state over the rest of the study period, while phosphorus mass was slowly immobilized throughout the steady-state phase.
Potassium mass decreased quickly during the first 3 months and then slowly decreased to 50% of the original mass. Thereafter potassium mass retained about 50% of the original mass throughout the rest of the study period. Magnesium mass rapidly decreased, probably due to leaching, during the first 3 months. Changes of calcium mass were similar to those of carbon, except with a mass increment during the first 3 months.

*Changes in Carbon to Nutrient ratios*

Fig. 2 shows the carbon to nutrient ratios during the decomposition periods. The carbon to nitrogen ratio (C/N) was 162 for the initial needle litter, then decreased to 154 during the leaching phase from 0 to 3 months. During the net immobilization phase from 3 to 9 months, the C/N ratio changed from 154 to 76, then the C/N ratio changed gradually from 76 to 36 during the period between 9 to 48 months. The carbon to phosphorus ratio (C/P) decreased quickly during the first 9 months and then slowly decreased through the rest of the study period. The carbon to potassium ratio (C/K) was variable throughout the study period. The carbon to magnesium ratio (C/Mg) was also variable throughout

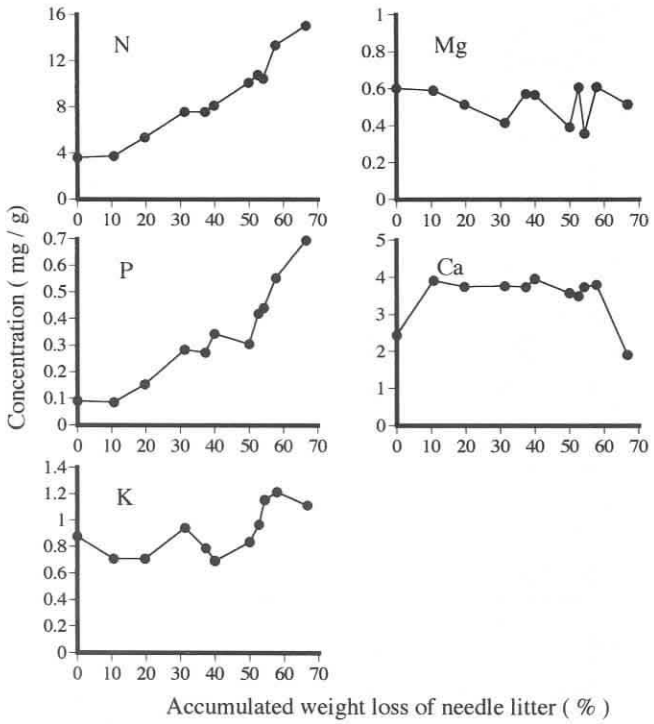


**Fig. 3.** Changes in concentrations of nutrients in relation to accumulated litter mass loss for needle litter

the experimental period and there were no remarkable differences of the ratios between the initial and final litter samples. The carbon to calcium ratio (C/Ca) was in a steady-state throughout the study period with the exception of the initial and final litter samples.

*Changes in nutrient concentrations*

Fig. 3 shows the changes in concentrations of nutrient in relation to accumulated mass loss of pine needles. The concentrations of N and P increased linearly with accumulated mass loss. The correlation coefficients between litter mass loss and concentrations of N and P were positive (Table 2). The results showed a strong retention of N and P in the decomposing litter during the study period. The concentrations of K were decreased in the first 3 months and then increased during the rest of the study period. The coefficient between litter mass loss and concentration of K was positive. The concentrations of Mg and Ca showed no significant correlation with the litter mass losses during the study period.

**Table 2.** Correlation coefficients for linear relations between accumulated litter mass loss and concentration of some nutrients

| Nutrient | Coefficients of correlation |
|---|---|
| N | 0.966*** |
| P | 0.934*** |
| K | 0.654* |
| Mg | −0.082 |
| Ca | −0.278 |

* $p < 0.05$; *** $p < 0.001$

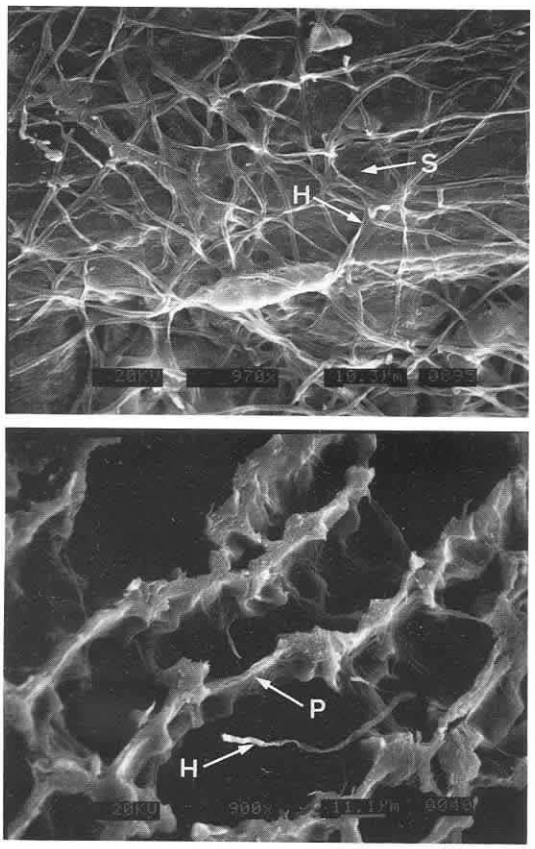


**Fig. 4.** Electron micrographs of pine needles with the fungal colonization. (a) The fungi colonizing the wax and epidermis layers on the surface of the needles. (b) The fungi colonizing into the palisade tissues of the needles. H; Hypha of fungi, S; Surface layer of the needle, P.; Cell wall of the palisade cell

*Changes in fungal abundances of the surface and internal tissues of needles*

Observation by SEM revealed the fungal colonization of the surface and internal tissues of needles. Fig. 4 (a) shows the fungi colonizing the wax and epidermis layers on the surface of the needles. Fig. 4 (b) shows the fungi colonizing into the palisade tissues of the needles.

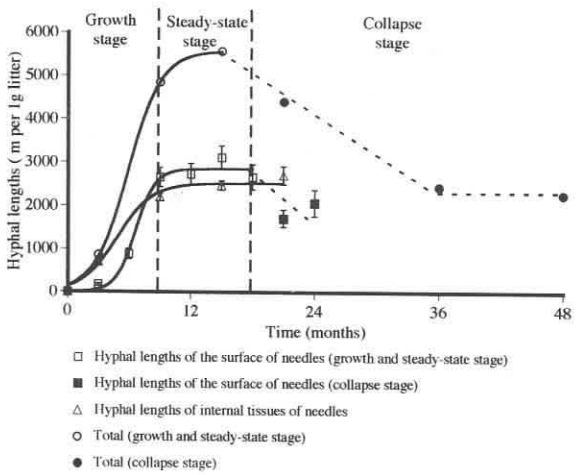


**Fig. 5.** Changes in the hyphal lengths during 4 years of decomposition. For the 3rd and 4th year samples the hyphae of the surface and internal tissues of needles cannot be separated because of fragmentation

Fig. 5 shows the changes in hyphal lengths of the surface and internal tissues of needles and total lengths during decomposition processes. Fungal colonization on the surface of needles was characterized by three stages as follows; stage 1: growth (3 to 9 months), stage 2: steady-state (12 to 18 months), and stage 3: collapse (21 to 48 months). During stage 1 to 2, the hyphal lengths of the surface of needles were significantly related to the C/N and C/P ratio (for C/N, $p < 0.01$, $r = -0.935$, d.f. = 4, for C/P, $p < 0.01$, $r = -0.947$, d.f. = 4), suggesting the immobilization of nitrogen and phosphorus by fungal growths on the surface of needles, i.e. wax and epidermis layers.
The hyphal lengths of the internal tissues of needles increased from 693 m/g at 3 months to 2694 m/g at 21 months. Hyphal lengths of the internal tissues of needles increased rapidly during the period from 0 to 9 months, as was the case of the surface fungi, then the increasing rate was low during the rest of the study period. The total hyphal lengths at the 36th and 48th month decreased to about 2000 m/g. This suggests that the 3rd and 4th year litter were also in the collapse stage of hyphal lengths.

*Colonization process of soil animal populations*

Table 3 shows the relative abundances of soil animal groups in the litter bags. Cryptostigmata (Acari) and Collembola were predominant groups in the litter bag fauna and each accounted for 33.7% and 31.6% of the total animal abundances, respectively.
Fig. 6 shows the changes in the densities of soil animal groups during the study period. Densities of soil animals were expressed by the number of individuals per gram of pine litter. The densities of total soil animals increased during the first 15 months and attained

**Table 3.** Abundances of soil animals colonizing the litter bags during the study period

| Group | Population density ($m^{-2}$) | Standard errors | Relative abundance (%) |
|---|---|---|---|
| Cryptostigmata | 4045.5 | 694.0 | 33.707 |
| Collembola | 3796.0 | 440.2 | 31.629 |
| Mesostigmata | 1334.8 | 281.6 | 11.122 |
| Astigmata | 1251.3 | 295.0 | 10.426 |
| Prostigmata | 938.3 | 300.1 | 7.818 |
| Diptera | 305.3 | 55.2 | 2.544 |
| Thysanoptera | 114.0 | 67.7 | 0.950 |
| Enchytraeidae | 99.5 | 40.2 | 0.829 |
| Psocoptera | 59.0 | 43.2 | 0.492 |
| Diplopoda | 18.8 | 9.5 | 0.157 |
| Coccoidea | 6.5 | 5.2 | 0.054 |
| Coleoptera | 4.5 | 2.1 | 0.037 |
| Araneae | 4.5 | 2.1 | 0.037 |
| Lepidoptera | 4.5 | 2.7 | 0.037 |
| Pseudoscorpiones | 4.0 | 1.3 | 0.033 |
| Amphipoda | 3.5 | 2.6 | 0.029 |
| Chilopoda | 3.0 | 2.1 | 0.025 |
| Symphyla | 2.3 | 1.4 | 0.019 |
| Pauropoda | 2.0 | 1.2 | 0.017 |
| Protura | 1.5 | 1.1 | 0.012 |
| Opiliones | 1.0 | 0.7 | 0.008 |
| Hymenoptera | 1.0 | 0.7 | 0.008 |
| Isopoda | 0.5 | 0.5 | 0.004 |
| Haprotaxida | 0.5 | 0.5 | 0.004 |
| Total | 12001.8 | | |

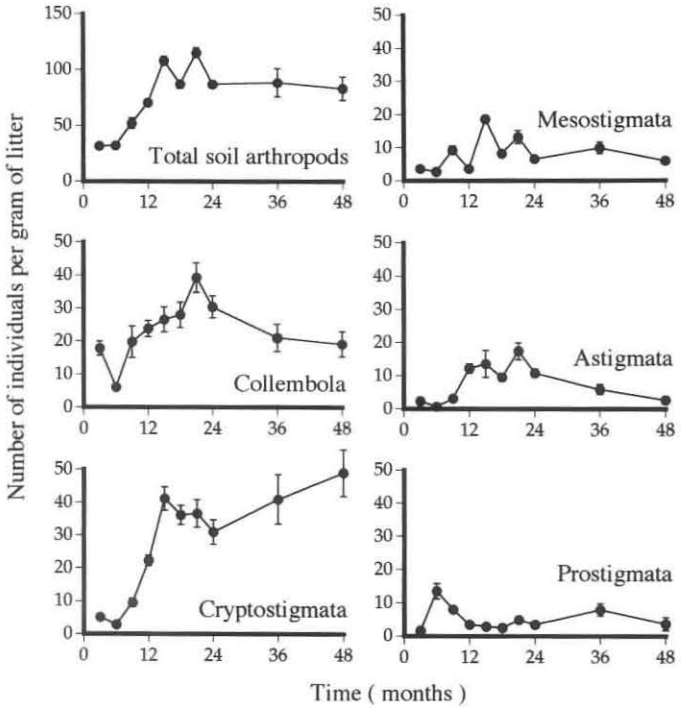


**Fig. 6.** Changes in the number of individuals of the main soil animal groups per gram of needle litter Bars indicate standard errors

a maximum of 115 individuals per gram in the 21 month litter bags. Then the densities decreased to about 85 individuals and were in steady-state throughout the rest of the study period.

The densities of Collembola were 20 individuals per gram even at the 3rd month and decreased at the 6th month because of summer drought in 1990. Then the densities rapidly increased to a maximum of 39 individuals at 21 months. During the rest of the study period, the collembolan densities were about 20 individuals per gram.

The densities of Cryptostigmata were low in the 3 and 6 month samples and then rapidly increased until the first peak at 15 months. After the peak density, Cryptostigmata decreased during a 12 month period. The densities of Cryptostigmata increased from 24 months to the end of the study period. Mesostigmata and Astigmata were later colonizers compared to Collembola. In Prostigmata, the density showed a peak in the 6-months litter bags.

*The correlation between abundances of soil arthropods and carbon/nutrient ratios*

The carbon to nutrient ratios represent the resource quality of litter for the soil animals. So, the correlation coefficients between densities of soil arthropods and carbon/nutrient ratios were examined. There were significant relationships between total soil arthropod densities and C/N and C/P ratio (for C/N, $p < 0.01$, $r = -0.772$, d.f. $= 8$; for C/P, $p < 0.05$, $r = -0.767$, d.f. $= 8$). Among the soil animal groups, Cryptostigmata showed significant correlations between the densities and C/N and C/P ratios (for C/N, $p < 0.01$, $r = -0.832$, d.f. $= 8$; for C/P, $p < 0.01$, $r = -0.771$, d.f. $= 8$). There were negative correlations between densities of other soil animal groups and C/N and C/P ratios, except for Prostigmata, but the correlation coefficients were not significant at the level of $p < 0.05$.

**Table 4.** Characteristics of two decomposition phases, i.e. the early phase from 3 to 18 month and the late phase from 21 to 48 months, in terms of carbon and nutrient states (N, P), fungal abundances and soil animal densities

| Decomposition phase | early phase | | late phase |
|---|---|---|---|
| Time (months) | 3–9 | 12–18 | 21–48 |
| Fungal condition | growth stage | steady-state stage | collapse stage |
| Hyphal lengths (m/g. d. wt. of litter) | 2848(858–4837) | 5557 | 3022(2247–4394) |
| Nitrogen and phosphorus state | leaching rapid immobilization | steady-state | steady-state |
| Carbon loss rate (mg C/month) | 57 | 37 | 8.5 |
| Animal density (g. d. wt. of litter) | | | |
| Total soil animal | 38.5 | 88.4 | 93.2 |
| Collembola | 14.5 | 26.1 | 27.4 |
| Cryptostigmata | 5.8 | 33.2 | 39.3 |

## Discussion

### *Changes in litter weights during the decomposition*

Table 4 shows the relation between fungal condition, nutrient dynamics and animal density during the study period. In this study, the decomposition rates of pine needles decreased with the field exposed time and were significantly higher in the early decomposition phase than in the late decomposition phase. Carbon loss rates were higher in the early decomposition phase than the late decomposition phase. Long term study of coniferous litter has shown a retarded decomposition rate during the late decomposition phase (Berg et al. 1982; Takeda 1988, 1995). In the late decomposition phase, the decreases in decomposition rates over time have been explained by the increases of refractory components in the decomposing litter (Berg & Ågren 1984). Berg (1986) suggested that decomposition of litter may be divided into at least two phases. In the first phase soluble substances and non-lignified carbohydrates (cellulose and hemicellulose) are decomposed by saprotrophic fungi. In the late decomposition phase, on the other hand, primarily lignin and lignified cellulose remain.

### *Changes in nutrient mass during the decomposition*

In this study, nutrient dynamics of decomposing litter were categorized into three types. The first type was characterized by the leaching loss in the first 3 months of decomposition process. In this study, potassium showed such a type. The second type showed changes in amounts similar to those in needle weights, as in the cases of Ca and Mg. Nitrogen and phosphorus showed a third type, which was characterized by the increases of the concentrations and absolute amounts during decomposition. This type of nutrient, such as nitrogen and phosphorus, has been suggested to limit the growth of microbial populations in some studies (Staaf & Berg 1982; Berg & Söderström 1979; Bååth & Söderström 1979; Ausmus et al. 1976). During the pine needle decomposition processes, the leaching, accumulation and final release phase of nutrients are distinguished for the limiting nutrients

such as N and P (Berg & Staaf 1981). In this study, nitrogen and phosphorus followed the leaching, immobilization and steady-state phase. But no mobilization of N and P occurred even at the end of this experiment.

*Nitrogen and Phosphorous dynamics in relation to fungal colonization*

The dynamics of limited nutrients have been related to nutrient and carbon utilization by the microbial populations (Berg & Staaf 1981). In this study, the fungal colonization patterns were characterized by three stages as follows: 1). growth stage during 3 to 9 months, 2). steady-state stage during 12 – 18 months, and 3). collapse stage during 21 to 48 months.
Table 4 shows that fungal populations contributed to both the net immobilization of nitrogen and phosphorus during the growth stage. Nitrogen and phosphorus were strongly immobilized in the growth stage, during which immobilization rates exceeded the mobilization rates of nutrients. During the steady-state stage, N and P amounts remained in a steady-state, while the carbon mobilization continued. During this stage, immobilization rates of nutrients were balanced by the mobilization rates. The carbon loss rate decreased during the collapse stage, fungal population reduced their abundances but the nitrogen and phosphorus were well retained in the litter until the end of experiment. In this stage, the decomposition process may be controlled by the availability of carbon sources derived from the decomposition of lignin and other refractory carbon (Berg 1986). Thus, the immobilization and mobilization of N and P were balanced with low activities of saphrotropic microbial populations during the late decomposition phase.

*Changes in soil animal abundances*

In mor and moder humus forms, Collembola and Acari are major decomposers (Petersen & Luxton 1982). In this study, the litter bag fauna mainly consisted of Collembola and Acari. Faunal abundances per gram of litter increased with the phase of decomposition, which suggests that the litter bags provided favourable physical and food conditions for the colonization of soil animals. Other studies have also reported an increase in faunal abundance with the advance of decomposition (Hågvar & Kjøndal 1981; Seastedt and Crossley 1983; Takeda 1988, 1995).
The importance of litter moisture has often been shown for the colonization of Collembola (Joose & Veltkamp 1970; Verhoef & Witteveen 1980; Vegter 1983) and Cryptostigmata (Lebrun 1969). In this study low moisture content in the litter probably inhibited colonization by microarthropods, resulting in low density levels in the first year. Density of soil animals in a litter bag increased in the second year and remained fairly constant over the study period. Litter falls in the winter covered the litter bags and thus environmental extremes in temperature and moisture were ameliorated for the colonization of soil animals.

*The roles of soil animals in decomposition processes*

In this study, faunal abundances were not correlated with the decomposition rates during the decomposition processes. Takeda (1988) suggested three explanations for the decrease in decomposition rates with increasing decomposer abundances as follows; (1) indirect effect of soil animals on decomposition, (2) recycling of organic matter and (3) methodological problems of litter bag.
In the immobilization phase, the soil animals may control the microbial metabolism through their grazing activities (Hasegawa & Takeda 1995). Such effects have been demonstrated for Collembola in the laboratory (Hanlon & Anderson 1979; Ineson et al. 1982; Setälä

et al. 1991). Animal grazing activities during the immobilization phase may also be limited by predation pressures and environmental variability, such as drought in this study. During the immobilization phase, grazing activities of soil animals may be too low to completely use the fungal biomass. This low level of grazing during the immobilization phase may promote the immobilization of nitrogen and phosphorus by fungal decomposers. Thus, Collembola and Acari contributed indirectly to the decomposition process by their grazing effects on fungal communities.

After the collapse stage of the fungal community, the needles entered into the late decomposition phase (Table 4). The late decomposition phase might be controlled by the utilization of refractory components such as lignin material by microbial and animal populations (Berg 1986). Lignin-degrading fungi need another C source to decompose lignin (Kirk et al. 1976). Thus, in the late decomposition phase, the microbial activities may be limited by the carbon sources. So, the carbon sources for the microbial decomposition may be supplied from the cellulose exposed by the comminution of soil animals.

Table 4 shows the increase of Cryptostigmata abundance in the late decomposition phase. A species of phthiracarid mite *(Hoplophthiracarus pavidus)* increased in the late decomposition phase of this study. These mites feed mainly upon mesophyll cells and deposit faeces in the feeding cavity within needles. Takeda (1995) showed that the number of feacal pellets of Cryptostigmata and needles attacked by Cryptostigmata increased exponentially with the advance of decomposition. In the late decomposition phase, detritus-feeding Collembola increased their abundances (Hasegawa & Takeda 1995). This feeding by Cryptostigmata and Collembola may increase the exposed site of organic matter for microorganisms. The detritus and endophagous feeder might be important for the carbon and nutrient mobilization of coniferous litter in the late decomposition phase. The detritus feeding might contribute to the recycling of organic matter such as animal faeces and decomposition products.

The moder humus form is characterized by microarthropod faecal aggregates in the F layer (Bal 1970; Green et al. 1993). Thus, carbon and nutrients of litter slowly mobilized through the recycling of organic matter in the F layer. The grazing effect of the animals might occur mainly in the early decomposition phase, when the microbial activity is high, while the comminution effect may be important in the late decomposition phase. The grazing effects of Collembola and Cryptostigmata on the immobilization phase of litter have been emphasized in the literature (Verhoef & Brussard 1990), while the effects of soil arthropods on the late decomposition phase are still unclear. More detailed studies of the late decomposition phase and the roles of micro-organisms and soil animals are needed to clarify the carbon and nutrient dynamics in the recycling systems of soils.

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